NEW FOSSIL POLYPTERIDAE FROM THE CENOMANIAN OF SUDAN. AN EVIDENCE OF THEIR HIGH DIVERSITY IN THE EARLY LATE CRETACEOUS

by

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ABSTRACT. - The Cenomanian ichthyofauna of the continental Wadi Milk Formation in northern Sudan comprises fourteen species of polypterids. They represent seven new species which are referred to five genera. A new Cenomanian species of the Recent genus *Polypterus* expands the range of this living taxon back to the early Late Cretaceous. The new discoveries both in Niger and Sudan as well as their phylogenetic implications led to the splitting of the genus *Sainthilairia* Gayet & Meunier, 1996, originally reported from Coniacian-Santonian sediments of In Becetem (Niger), into three genera (*Saharichthys*, *Sainthilairia* and *Inbecetemia*). The Cenomanian polypterids of the Sudan show an extraordinary diversity of this group at the time of their 'first' appearance.

RÉSUMÉ. - Nouveaux Polypteridae fossiles du Cénomanien du Soudan, une preuve de leur grande diversité au début du Crétacé supérieur.

L'étude de l'ichtyofaune du Cénomanien de la Formation Wadi Milk (Soudan) a permis la découverte de quatorze espèces de Polyptères, dont sept nouvelles regroupées en cinq genres. Une nouvelle espèce de *Polypterus* confirme la présence de ce genre actuel dès la base du Crétacé supérieur. Le genre *Sainthilairia* Gayet & Meunier, 1996, décrit dans le Coniacien-Santonien d'In Becetem (Niger) doit, en raison de nouvelles découvertes tant au Niger qu'au Soudan et d'arguments phylogénétiques, être éclaté en trois genres (*Saharichthys*, *Sainthilairia* et *Inbecetemia*). Les découvertes soudanaises montrent l'extrême diversité de ce groupe dès sa "première" apparition connue.

Key-words. - Polypteridae, Cretaceous, Cenomanian, Sudan, Morphology, Taxonomy, New taxa.

The polypterids are a relatively small group of fishes living in the fresh waters of Africa. Although they show many primitive characters, indicating a long fossil history, the phylogenetic evolution of the polypterids is poorly known. Recently, Meunier and Gayet focused on a study of osteology of recent polypterids, in a first step, on the spines of the dorsal fins; they investigated in detail the dorsal pinnulae of all living species and sub-species of the family Polypteridae including two genera (Meunier and Gayet, in prep.). The findings of this study combined with the results of the recovering and examination of the spines of dorsal fins from the Coniacian-Santonian of In Becetem (Niger) led to the discovery of three fossil genera and ten species (Gayet and Meunier, 1996a). The taxonomic description of these fossil polypterids is based on the anatomy of the pinnulae only. By comparing fossil and living morphotypes, it is possible to recognise male and female morphotypes in the fossil material. Furthermore, the fossil specimens of

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Niger enable the reconstruction of ontogenetic stages from juveniles to adults for each species (Gayet *et al.*, in prep.).

Other records of fossil polypterids, older than those of Niger, derive from the Cenomanian of Egypt (Stromer, 1936; Schaal, 1984) and, more recently, from the Cenomanian of Sudan (Werner, 1994a), and of Morocco (Sereno *et al.*, 1996). Younger records of polypterids in Africa are more frequent, e.g. from the Miocene of Kenya (Greenwood, 1951) and Tunisia (Greenwood, 1973), from the Pliocene of Egypt (Greenwood, 1972), from the Pleistocene of Ethiopia (Arambourg, 1948) and from the Holocene of Mali (Van Neer and Gayet, 1988).

Although the fossil polypterid pinnulae from Sudan are not so numerous as those from Niger, they occur in abundance and represent new taxa introduced here. Only the well preserved spines, without any trace of abrasion, are taken into consideration here. In view of the new material from the Cenomanian of Sudan, diagnostic characteristics of the pinnulae observed in the taxa from the Coniacian-Santonian of Niger are completed and improved here.

The high diversity of the Sudanese polypterids provides basic information for a better understanding of the evolution of the polypterid pinnulae and subsequently contributes to the illumination of the fossil history of these fishes.

A morphological study of pinnulae of living polypterids will soon be submitted by Meunier and Gayet. Additionally, a monograph dealing with all African and South American polypteriform fossils is in preparation (Gayet *et al.).* These works will include extended anatomical descriptions as well as detailed examinations of specimen, sexual, ordinal (related to the position of the pinnulae in the dorsal fin) and ontogenetic variations. However, the aim of the present paper is to briefly introduce the new discoveries in order to emphasise the importance of polypterid diversity.

Provenance of the material

The fish elements described here originate from the vertebrate-bearing locality situated in northern Sudan, about 200 km north-west of Khartoum (Fig. 1). In this place, the basal part of the outcropping Wadi Milk Formation is exposed by fine-grained multicoloured layers of 15 m in thickness. These fluvio-lacustrine horizons produced vertebrate remains in abundance. They are overlaid by coarser-grained series of the braided river systems of the Wadi Milk Formation (Bussert, 1993a, b).

Compiling all available data, Wycisk (1991) suggested an Albian to Cenomanian age for the Wadi Milk Formation. The Cenomanian age of the vertebrate-bearing layers was supported by the presence of the shark *Asteracanthus aegyptiacus* Stromer, 1927, up to date, only known from the Cenomanian Bahariya Formation in Egypt (Werner, 1994a).

Moreover, the sedimentary cycles of the Wadi Milk Formation show convincing similarities with those of the Omdurman Formation which crops out in the Khartoum area (Bussert, pers. comm.). The Omdurman Formation is subdivided into two members (Awad, 1994). The Umm Badda Member in the subsurface consists of fine-grained sediments of a meandering river facies. Palynological data indicate a late Albian to Cenomanian age (near the surface) for this member (*ibid.*). The exposed Merkhiyat Member is composed mainly of coarse-grained sandstones interpreted as being deposited by braided rivers. Its macrofloral content is indicative for a ?Turonian to Early Senonian age (*ibid.*). The correlation of the palynologically dated Umm Badda Member with the fine-grained basal parts of the outcropping Wadi Milk Formation emphasises the Cenomanian age of the vertebrate-bearing horizons.

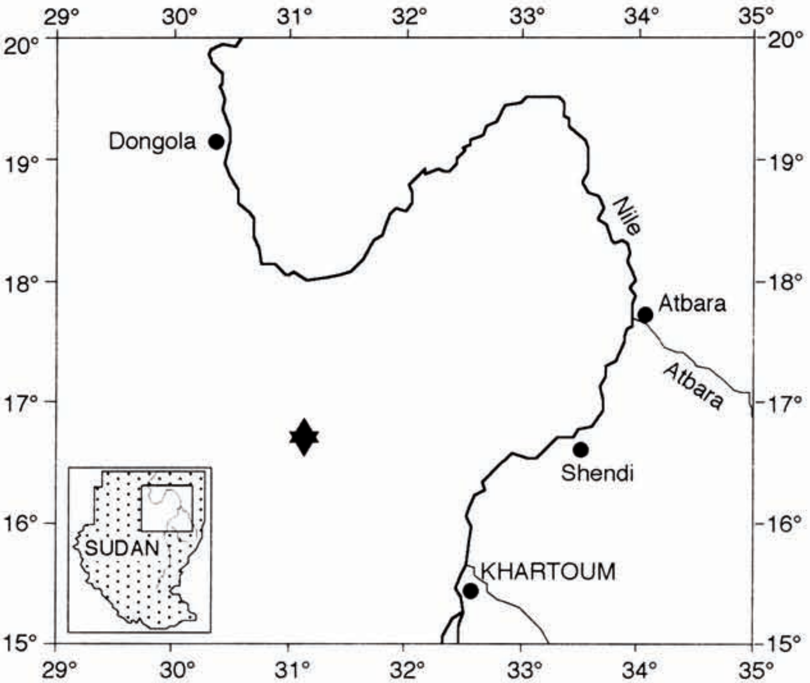


Fig. 1. - Location map of the vertebrate-bearing locality of Sudan.

Vertebrate association

The screen washing activities of more than seven tons of sediment as well as the collecting from the weathered surface yielded the most divers vertebrate fauna from the Cretaceous of Africa (Werner, 1994a). In this Cenomanian vertebrate assemblage, represented exclusively by non-articulated elements, aquatic and amphibious animals clearly predominate. The dinosaurs as the terrestrial elements include two titanosaurs, an undefinable other sauropod, two charcharodontosaurs, a questionable hypsolophodontid, *Ouranosaurus*, and another indeterminable iguanodontid (Rauhut, 1995). A dromaeosaurid theropod represents the first record of this dinosaur family on Gondwanian continents (Rauhut and Werner, 1995). Thus the dinosaur assemblage shows an extraordinary diversity. The herpetofauna includes different long- and medium-snouted mesosuchian crocodiles and at least three erymnochelyine turtles. The snakes comprising a total of seven taxa belong to the oldest findings in this vertebrate group and therefore are surprisingly divers (Werner and Rage, 1994). In the Cenomanian of Sudan, lissamphibians occur with all three major groups: frogs, gymnophionans (Werner, 1994b) and salamanders (Evans *et al.*, 1996). The gymnophionans are the oldest ones reported from Gondwana. The salamanders are the earliest sirenids and the first sirenids known outside North America (*ibid.*).

The fish fauna found in the Wadi Milk Formation is very rich, but it has yet to be studied in detail (Werner, 1994a). A few remains of elasmobranchs occur: a fragment of a fin spine and three teeth of the fresh water shark *Asteracanthus aegyptiacus* Stromer, 1927, as well as one tooth of a not yet named new batoid.

About 500 lungfish tooth plates of different sizes were found in the Cenomanian of Sudan. Thanks to the great quantity of the specimens, Gloy (1997) reconstructed ontogenetic series from embryonic to senile stages of the fossil *Protopterus humei* (Priem, 1914) and of a new species of *Protopterus*. The tooth plates of *Protopterus protopteroides* (Tabaste, 1963), *Ceratodus carinatus* Schaal, 1984, *C. casieri* Cappetta, 1972, and *Protopterus*? *regulatus* Schaal, 1984, reflect different stages in the ontogenetic series of *Protopterus humei* and therefore represent junior synonyms of *P. humei* (Gloy, 1997). The third Sudanese lungfish is represented by one tooth plate of *Neoceratodus tuberculatus* (Tabaste, 1963).

Apart of indeterminable ichthyoliths, fish teeth and vertebrae (most probably teleosts) in abundance, one characiform tooth is recognized (Werner, 1994a) in the Wadi Milk Formation. The presence of osteoglossids in the Cenomanian of Sudan is indicated by many sculptured dermoskeletal squamules of polygonal outline. Lepisosteids are characterised by the presence of their ganoid scales and opisthocoelous vertebrae. The occurrence of polypterid scales and fin spines was already mentioned by Werner (1994a), but the enormous variations observed in the shape of the basal parts of the pinnulae was interpreted as probably being related to the different articulation positions of the spines at the fish body. To clarify this wrong interpretation, the polypterid spinnulae are studied in this paper.

The specimens figured and described here are housed in the collection of the Special Research Project (SFB 69) of the Technical University of Berlin (TUB-SFB69).

SYSTEMATIC RESULTS
CLASS CLADISTIA, ORDER POLYPTERIFORMES, FAMILY POLYPTERIDAE

The original diagnoses of the living polypterid taxa did not include morphological characters of the pinnulae, except for their number and/or their dorsal position. We do not change any characters of these original diagnoses. However, we complete the diagnoses of the living taxa by integrating the morphological characters of the pinnulae. This is obligatory in view of the fossil record of polypterids which are represented mainly by pinnulae.

ERPETOICHTHYS (SMITH, 1866)

Emended diagnosis (in part: spine of pinnulae only). - Polypteridae in which the articular head of the dorsal fin spine has no individualised processes.

Type-species. - *Erpetoichthys calabaricus* (Smith, 1866). Recent.

Comment. - All fossil polypterid dorsal spines either from Niger or from Sudan show well differentiated processes so that this genus is not known by Cretaceous records so far.

POLYPTERUS GEOFFROY SAINT-HILAIRE, 1802

Emended diagnosis (in part: spine of pinnulae only). - Polypteridae in which the basal processes are laterally fixed; more or less long posterior processes of the dorsal fin spine with or without distal depression which coalesce with the basal processes; articular

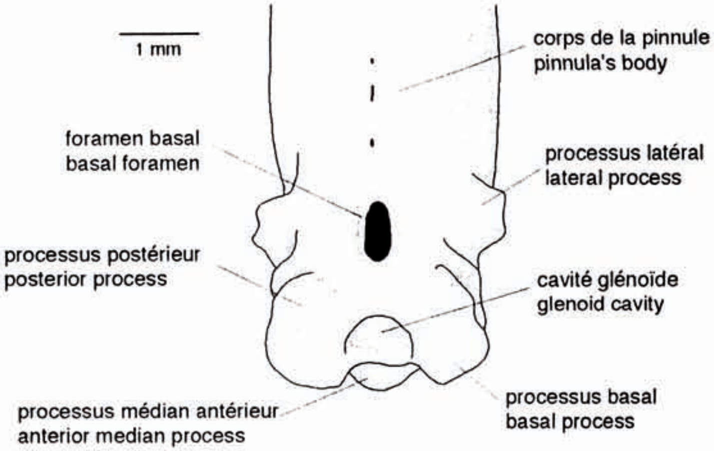


Fig. 2. - Dorsal fin spine of *Polypterus senegalus* in posterior view.

head rectangularly (higher than wide), trapezoidally or triangularly shaped in posterior view; anterior median process more or less developed independently of the ordinal rank of the pinnula; glenoid cavity not surrounded by bony pad; alveolar tissues absent; articulation of the spine with a pterygiophore in the glenoid cavity; lateral symmetry of the body of the spine without any twisting (Fig. 2).

Type species. - *P. bichir bichir* Geoffroy Saint-Hilaire, 1802. Recent.

Polypterus dageti Gayet & Meunier, 1996

1996a *Polypterus dageti.* Gayet and Meunier, *C. R. Acad. Sci., Paris*: 703-704, fig. 2a.

Diagnosis. - *Polypterus* with well individualised anterior median process which can cross the inferior limit of the basal processes, according to the ordinal rank of the pinnulae in the dorsal fin.

Comment. - The specimens of *P. dageti* are few in number in both localities but less numerous in Sudan (about 6) than in Niger (about 15).

Polypterus sudanensis nov. sp. (Fig. 3)

Diagnosis. - Dorsal fin spine of *Polypterus* with very long tubular posterior processes joining the basal processes at the base of the spine and hiding them in posterior view; posterior processes with deep depressions at their distal extremity.

Holotype. - Basal part of the pinnula Vb-1009.

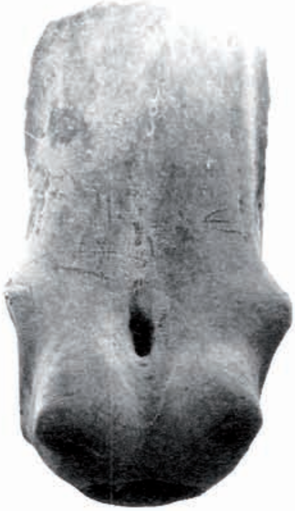
Type locality. - C. 200 km north-west of Khartoum, Sudan (map reference: 31°8.7'E; 16°41.7'N).

Type strata. - Basal part of the outcropping Wadi Milk Formation.

Age. - Cenomanian.

Derivation of the specific name. - After Sudan, the country of origin.

Occurrence. - This species is known in Sudan only (about 10 specimens).



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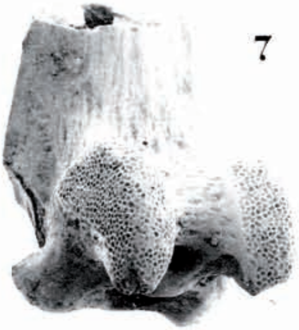

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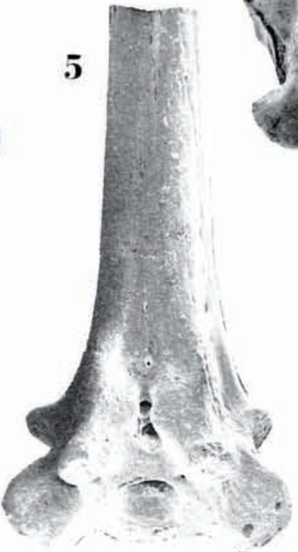

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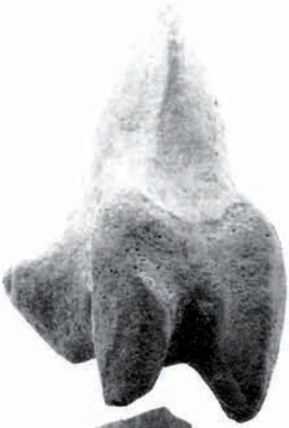

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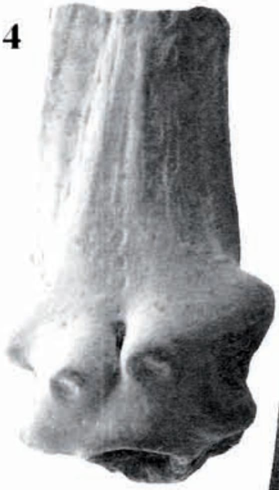

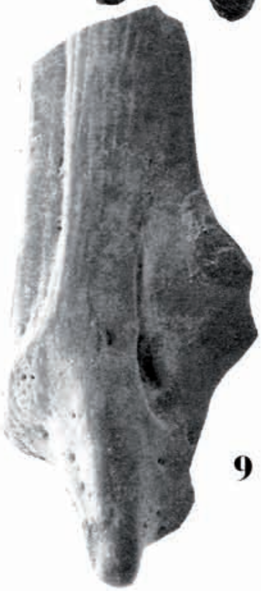

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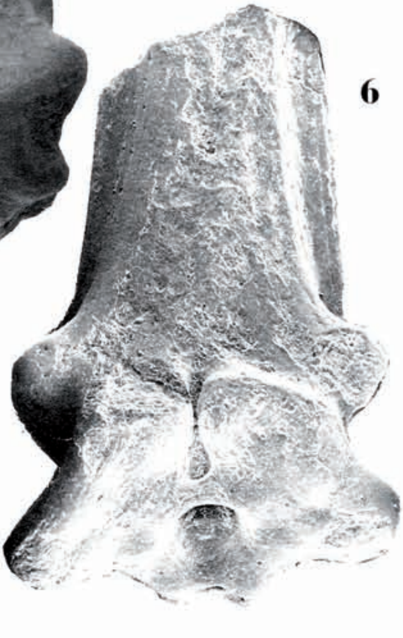

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0,5 mm

BARTSCHICHTHYS GAYET & MEUNIER, 1996

1996a *Bartschia.* Gayet and Meunier, *C. R. Acad. Sci., Paris*: 704, figs. 2b, c.

1996b *Bartschichthys.* Gayet and Meunier, *Cybium*, 20(3): 314 (new name).

The generic name *Bartschia* proposed by Gayet and Meunier (1996a) for a Coniacian-Santonian polypterid of In Becetem (Niger) was preoccupied by a gastropod (Mollusca). Therefore, *Bartschichthys* was proposed as a replacement (Gayet and Meunier, 1996b).

Emended diagnosis. - Polypteridae in which the articular head is inversely trapezoid-shaped in posterior view, resulting from the laterally well pronounced lateral processes and a quite non-accentuated lateral development of the basal processes; small and smooth bullet-like posterior processes in median position, sometimes basely well developed; alveolar tissues absent; glenoid cavity without bordering pad; lateral symmetry of the body of the spine sometimes slightly twisted; articulation of the spine with a pterygiophore in a glenoid cavity.

Type species. - *Bartschia arnoulti* Gayet & Meunier, 1996, from the Coniacian-Santonian of In Becetem (Niger).

Bartschichthys arnoulti (Gayet & Meunier, 1996)

1996a *Bartschia arnoulti.* Gayet and Meunier, *C. R. Acad. Sci., Paris*: 704, fig. 2b.

1996b *Bartschichthys arnoulti* (Gayet & Meunier). Gayet and Meunier, *Cybium*, 20(3): 314 (new name).

Emended diagnosis. - Dorsal fin spines of *Bartschichthys* in which the lateral processes are separated from the posterior ones; rounded off posterior processes without depression at their distal extremity; lateral and posterior basal processes isolated; basal processes always with a slight lateral development, which is not related to the ordinal position of the pinnula; distance between the lateral limits of the basal processes just a little more wider than the distance between the lateral limits of the body of the spine; anterior ganoid surface never extended below the basal transversal process; no separated ridges on the ganoin.

Occurrence. - This species is known very few in number in Sudan (2 specimens) and numerous in Niger (more than 40 specimens).

Fig. 3. - *Polypterus sudanensis* nov. sp., holotype Vb-1009, Wadi Milk Formation Sudan, dorsal fin spine in postero-lateral view.

Fig. 4. - *Bartschichthys napatensis* nov. sp., holotype Vb-1010, Wadi Milk Formation Sudan, dorsal fin spine in postero-lateral view.

Fig. 5. - *Sudania gracilis* nov. gen., nov. sp., holotype Vb-696, Wadi Milk Formation Sudan, dorsal fin spine in posterior view.

Fig. 6. - *Sudania oblonga* nov. gen., nov. sp., holotype Vb-695, Wadi Milk Formation Sudan, dorsal fin spine in posterior view.

Fig. 7. - *Sainthilairia intermedia* nov. sp., holotype Vb-1013, Wadi Milk Formation Sudan, dorsal fin spine in postero-lateral view.

Fig. 8. - *Sainthilairia elongata* nov. sp., holotype Vb-1014, Wadi Milk Formation Sudan, dorsal fin spine in postero-lateral view.

Fig. 9. - *Nagaia extrema* nov. gen., nov. sp., holotype Vb-1015, Wadi Milk Formation Sudan, dorsal fin spine in postero-lateral view.

Bartschichthys napatensis nov. sp. (Fig. 4)

Diagnosis. - Dorsal fin spine of *Bartschichthys* with basely developed posterior processes showing depressions at their distal extremity; lateral and posterior processes isolated; the lateral development of the basal process closely related to the ordinal position of the pinnula; basal foramen in a deep elongated groove situated between the two posterior processes; ganoin surface often reaching the basal transversal pad and with vertical separated ridges in its distal part.

Holotype. - Basal part of the pinnula Vb-1010.

Type locality. - C. 200 km north-west of Khartoum, Sudan (map reference: 31°8.7'E; 16°41.7'N).

Type strata. - Basal part of the outcropping Wadi Milk Formation.

Age. - Cenomanian.

Derivation of the specific name. - After the Napatan culture (c. 800 BC to c. 300 BC) of the territory of modern Sudan.

Occurrence. - Sudan only (about 16 specimens).

Bartschichthys tubularis (Gayet & Meunier, 1996)

1996a *Bartschia tubularis*. Gayet and Meunier, *C. R. Acad. Sci., Paris*: 704, fig. 2c.

1996b *Bartschichthys tubularis* (Gayet & Meunier). Gayet and Meunier, *Cybium*, 20(3): 314 (new name).

Diagnosis. - Small species of *Bartschichthys* in which ganoin covers nearly the whole body (all faces) of the dorsal fin spine; transversal section of the adult spine rhombic, higher than wide or as high as wide.

Comment. - This species is only known in Niger (about 22 specimens). However, we add this diagnosis to facilitate the morphological comparisons.

SUDANIA NOV. GEN.

Diagnosis. - Polypteridae in which articular head of the dorsal fin spine is rectangularly shaped and wider than high; lateral and basal processes well developed with strong laterally directed pronunciations; lateral and basal processes separated from each other by a more or less deep lateral depression; alveolar tissues absent; glenoid cavity without pad; lateral symmetry of the body, sometimes slightly twisted; articulation of the spine with a pterygiophore in a glenoid cavity.

Type species. - *Sudania gracilis* nov. gen., nov. sp. from the Cenomanian of the Wadi Milk Formation (Sudan).

Derivation of the generic name. - After Sudan, the country of origin.

Sudania gracilis nov. gen., nov. sp. (Fig. 5)

1994a Polypteridae. Werner, *Berliner geowiss. Abh.*, taf. 2, fig. 2.

Diagnosis. - Dorsal fin spine of *Sudania* with clearly distinct basal and lateral processes, situated more or less parallelly and symmetrically around the depression in between; head of spine flattened anterio-posteriorly; small and rounded off posterior processes in median position.

Holotype. - Basal part of the pinnula Vb-696.

Type locality. - C. 200 km north-west of Khartoum, Sudan (map reference: 31°8.7'E; 16°41.7'N).

Type strata. - Basal part of the outcropping Wadi Milk Formation.

Age. - Cenomanian.

Derivation of the specific name. - After the slender shape of the dorsal spine of this *Sudania* species.

Occurrence. - These species has been found in Sudan only (about 17 specimens).

***Sudania oblonga* nov. gen., nov. sp. (Fig. 6)**

1994a Polypteridae. Werner, *Berliner geowiss. Abh.*, taf. 2, fig. 1.

Diagnosis. - Dorsal fin spine of *Sudania* with oblong and longish basal processes, neither parallelly nor symmetrically placed in regard to the lateral processes; anterior face highly rounded off; longish posterior processes showing the same oblique direction as the basal processes.

Holotype. - Basal part of the pinnula Vb-695.

Type locality. - C. 200 km north-west of Khartoum, Sudan (map reference: 31°8.7'E; 16°41.7'N).

Type strata. - Basal part of the outcropping Wadi Milk Formation.

Age. - Cenomanian.

Derivation of the specific name. - After the oblong shape of both the posterior and lateral processes of the pinnula of this *Sudania* species.

Occurrence. - Sudan only (about 11 specimens).

SAHARICHTHYS NOV. GEN.

1996a *Sainthilairia* (in part). Gayet and Meunier, *C. R. Acad. Sci., Paris:* 704, figs. 3a, b.

Diagnosis. - Polypteridae in which alveolar tissues are developed on the posterior and lateral processes of the dorsal fin spine, as in the dorsal fin spines of the pinnulae of the genera *Sainthilairia* and *Inbecetemia*; posterior processes never basely developed; body of the spine sometimes twisted dextrally or sinistrally, but head of the spine always symmetric; articulation of the spine with pterygiophore in a glenoid cavity not surrounded by bony pad.

Type species. - *Sainthilairia nigeriensis* Gayet & Meunier, 1996 from the Coniacian-Santonian of In Becetem (Niger).

Derivation of the generic name. - After Sahara, the desert region of North Africa, and the Greek word for fish.

***Saharichthys nigeriensis* (Gayet & Meunier, 1996)**

1996a *Sainthilairia nigeriensis*. Gayet and Meunier, *C. R. Acad. Sci., Paris*: 705, fig. 3a.

Emended diagnosis. - Dorsal fin spines of *Saharichthys* with areas of alveolar tissues limited to the superior face of the posterior processes and the inferior face of the anterior ones; rounded and bulky posterior processes, ventrally never developed; double pads above and a depression below.

Occurrence. - These species has been found both in Sudan (about 7 specimens) and in Niger (about 11 specimens).

Saharichthys africanus (Gayet & Meunier, 1996)

1996a *Sainthilairia africana*. Gayet and Meunier, *C. R. Acad. Sci., Paris*: 704, fig. 3b.

Emended diagnosis. - Dorsal fin spines of *Saharichthys* with well developed areas of alveolar tissues on the whole surface of the posterior processes and on the inferior face of the lateral ones; rounded off and bulky posterior processes without pad above and without depression below.

Occurrence. - Niger only (about 8 specimens).

SAINTHILAIRIA GAYET & MEUNIER, 1996

1996a *Sainthilairia* (in part). Gayet and Meunier, *C. R. Acad. Sci., Paris*: 705, figs. 3c, d, e.

Emended diagnosis. - Polypteridae in which the posterior processes of the dorsal fin spine are very well developed and strongly curved; alveolar tissues on the whole posterior processes and on the inferior part of the lateral ones; glenoid cavity rounded, with or without a bony pad; sometimes dextrally or sinistrally twisted spine body, without any modification of the symmetry of the head; articulation of the spine made with a pterygiophore in the glenoid cavity.

Type species. - *Sainthilairia falciformis* Gayet & Meunier, 1996 from the Coniacian-Santonian of In Becetem (Niger).

Sainthilairia falciformis Gayet & Meunier, 1996

1996a *Sainthilairia falciformis*. Gayet and Meunier, *C. R. Acad. Sci., Paris*: 705, fig. 3d.

Emended diagnosis. - Dorsal fin spine of *Sainthilairia* with well developed posterior processes, thickened and scythe-like in shape, passing beyond the inferior limit of the basal processes; alveolar tissues developed in a band with parallel borders along the posterior processes and joining laterally the lateral processes, with or without fusion; wide but shallow anterio-lateral depressions; glenoid cavity surrounded with a bony pad.

Occurrence. - These species has been found both in Sudan (about 6 specimens) and in Niger (about 35 specimens).

Sainthilairia intermedia nov. sp. (Fig. 7)

Diagnosis. - Dorsal fin spine of *Sainthilairia* with posterior processes passing beyond the inferior limit of the basal processes (like in the spines of *Sainthilairia falciformis* and *S. grandis*); posterior and lateral processes well separated (like in the spines of *S. grandis*), lateral processes more laterally developed than the basal processes; alveolar tissue developed on the anterior face of the spine at the lateral processes level (like in the spines of *Saharichthys*).

Holotype. - Basal part of the pinnula Vb-1013.

Type locality. - C. 200 km north-west of Khartoum, Sudan (map reference: 31°8.7'E; 16°41.7'N).

Type strata. - Basal part of the outcropping Wadi Milk Formation.

Age. - Cenomanian.

Derivation of the specific name. - After the intermediate characteristics of the pinnulae between the ones of *Sainthilairia falciformis* and *S. grandis*.

Occurrence. - Sudan only (4 specimens).

Sainthilairia grandis Gayet & Meunier, 1996

1996a *Sainthilairia grandis*. Gayet and Meunier, *C. R. Acad. Sci., Paris*: 705, fig. 3e.

Emended diagnosis. - Very large species of *Sainthilairia*; dorsal fin spines with posterior processes similar to those of *Sainthilairia falciformis*, but alveolar plates of the lateral and posterior processes largely separated; basal processes more laterally developed than the lateral ones.

Occurrence. - Niger only (about 6 specimens).

Sainthilairia elongata nov. sp. (Fig. 8)

Diagnosis. - Dorsal fin spine of *Sainthilairia* with very long posterior processes passing beyond the inferior limit of the basal processes (like in the spines of *Sainthilairia falciformis, S. intermedia* and *S. grandis*); lateral and posterior processes largely separated (similar to the fin spines of *S. intermedia* and *S. grandis*, but in different proportions); strongly developed anterio-lateral depressions covering the whole surface between the lateral processes; basal processes absent; tubular body of the spine with an ogival transversal section; deep glenoid cavity without bony pad.

Holotype. - Basal part of the pinnula Vb-1014.

Type locality. - C. 200 km north-west of Khartoum, Sudan (map reference: 31°8.7'E; 16°41.7'N).

Type strata. - Basal part of the outcropping Wadi Milk Formation.

Age. - Cenomanian.

Derivation of the specific name. - After the elongated shape of the articular head of the dorsal fin spine.

Occurrence. - Sudan only (2 specimens).

Sainthilairia beccusiformis Gayet & Meunier, 1996

1996a *Sainthilairia beccusiformis*. Gayet and Meunier, *C. R. Acad. Sci., Paris*: 705, fig. 3c.

Emended diagnosis. - Dorsal fin spine of *Sainthilairia* with well developed distally pointed posterior processes separated by the lateral processes and never passing beyond the limit of the basal processes; glenoid cavity rounded with bony pad; no anterio-lateral depressions; transversal anterior pad joining the lateral processes.

Occurrence. - These species has been found both in Sudan (about 4 specimens) and in Niger (about 12 specimens).

INBECETEMIA NOV. GEN.

1996a *Sainthilairia* (in part). Gayet and Meunier, *C. R. Acad. Sci., Paris*: 706, figs. 4a, b, c.

Diagnosis. - Polypteridae with asymmetrical dorsal fin spines, dextrally or sinistrally twisted including strong asymmetry of the head; articulation of the spine by use of an extraordinarily developed basal process into a modified scale; second basal process regressed or disappeared; several patches of alveolar tissues; distorted glenoid cavity surrounded by bony pad.

Type species. - *Sainthilairia torta* Gayet & Meunier, 1996 from the Coniacian-Santonian of In Becetem (Niger).

Derivation of the generic name. - After In Becetem the locality of origin.

Inbecetemia torta (Gayet & Meunier, 1996)

1996a *Sainthilairia torta.* Gayet and Meunier, *C. R. Acad. Sci., Paris:* 705, figs. 4a, c.

Emended diagnosis. - Dorsal fin spine of *Inbecetemia* with the regressed basal process still present; development of a lateral bony plate; crescent-shaped articular pad of alveolar tissues; bulky posterior processes; distorted glenoid cavity surrounded by a bony pad; symmetrical origin of the spine still visible; scale for articulation with a transversal pad in mid high of the large articular cavity.

Occurrence. - Sudan (about 3 specimens) and Niger (about 20 specimens: 13 pinnulae and 7 articular scales). No articular scales have been found in the material of Sudan so far.

Inbecetemia tortissima (Gayet & Meunier, 1996)

1996a *Sainthilairia tortissima.* Gayet and Meunier, *C. R. Acad. Sci., Paris*: 705, fig. 4b.

Emended diagnosis. - Dorsal fin spine of *Inbecetemia* with well developed basal processes aligning in the axis of the body; regressed basal process always disappeared; lateral bony plate regressed; no crescent-shaped transversal articular pad; glenoid cavity small and distorted, surrounded by a bony collar-shaped pad; transversal section of the body nearly circular; scale for articulation with a single large cavity and without transversal pad.

Ocurrence. - Sudan (about 7 specimens) and Niger (about 61 specimens: 58 pinnulae and 3 articular scales). No articular scales have been found in the material of Sudan so far.

NAGAIA NOV. GEN.

Diagnosis. - Identical to the species *extrema.*

Type-species. - *Nagaia extrema* nov. gen., nov. sp. from the Cenomanian Wadi Milk Formation (Sudan).

Derivation of the generic name. - After the site Naga (Sudan) with its famous archaeological monuments.

Nagaia extrema nov. gen., nov. sp. (Fig. 9)

Diagnosis. - Dorsal fin spines with exaggerated development of the posterior processes, one of them becoming the articular process of the spine (probably in a specialised not yet known scale); glenoid cavity placed in between in a groove, very far away from the basal limit of the spine; basal processes deleted; regression of the alveolar tissues.

Holotype. - Basal part of the pinnula Vb-1015.

Type locality. - C. 200 km north-west of Khartoum, Sudan (map reference: 31°8.7'E; 16°41.7'N).

Type strata. - Basal part of the outcropping Wadi Milk Formation.

Age. - Cenomanian.

Derivation of the name. - After the extreme elongation of the posterior processes of the pinnula of this species.

Occurrence. - This species is known in Sudan (about 2 specimens) and by one pinnula in Niger.

DISCUSSION

The discovery of polypterids from the Cenomanian of the Wadi Milk Formation (Sudan) reveals new aspects of the history of these fishes. The results of morphological studies of these polypterid fin spines increase the number of known African fossil taxa of the family Polypteridae. At the same time they lead to a better understanding of the polypterids of the Coniacian-Santonian of Niger. The polypterids from the early Late Cretaceous sediments of Sudan comprises a total number of fourteen species including seven new species. The new genera *Saharichthys*, *Inbecetemia* and *Nagaia* occur both in the Cenomanian of Sudan and in the Coniacian-Santonian of Niger. While studying the fin spines of Niger, many morphological details characterising new taxa have been recognized. However, due to the rare material available in that time, many spines have been previously referred to as *Sainthilairia*. With the Sudanese spines showing the same diagnostic features, it was possible to split *Sainthilairia* into *Saharichthys nigeriensis* (Gayet & Meunier, 1996), *S. africanus* (Gayet & Meunier, 1996) and *Inbecetemia tortissima* (Gayet & Meunier, 1996). Some spines with the characteristics of the new genus *Nagaia* have also been found in the sediments of Niger before, but have not been named due to the rarity of the specimens. However, fin spines belonging to this genus were abundantly

Table I. - Occurrence of polypterid species in Niger (In Becetem) and Sudan (Wadi Milk Formation).

Taxa	Sudan	Niger
Polypterus		
P. dageti	•	•
***P. sudanensis* nov. sp.**	•	-
Bartschichthys		
B. arnoulti	•	•
***B. napatensis* nov. sp.**	•	-
B. tubularis	-	•
***Sudania* nov. gen.**		
***S. gracilis* nov. gen., nov. sp.**	•	-
***S. oblonga* nov. gen., nov. sp.**	•	-
Saharichthys		
S. nigeriensis	•	•
S. africanus	-	•
Sainthilairia		
S. falciformis	•	•
***S. intermedia* nov. sp.**	•	-
S. grandis	-	•
S. beccussiformis	•	•
***S. elongata* nov. sp.**	•	-
***Inbecetemia* nov. gen.**		
I. torta	•	•
I. tortissima	•	•
***Nagaia* nov. gen.**		
***N. extrema* nov. gen., nov. sp.**	•	•

found in the Cenomanian sediments of Sudan. Thus, many characteristics already realised in the material from Niger were recognized in Sudanese fin spines. The fact that there are more differences between the Cretaceous fin spines representing two species than between the spines of the two recent genera, strongly indicates the taxonomic significance of the spine morphology. Therefore, the study of both fin spines from Sudan and from Niger enabled generic and specific diagnosis.

General faunistic and palaecological similarities in the vertebrate assemblages of the Coniacian-Santonian of Niger and the Cenomanian of Sudan already have been pointed out (Werner, 1993). According to the recent results, the six polypterid species namely *Polypterus dageti* Gayet & Meunier, 1996, *Bartschichthys arnoulti* (Gayet & Meunier, 1996), *Saharichthys nigeriensis* (Gayet & Meunier, 1996), *Sainthilairia falciformis* Gayet & Meunier, 1996, *S. beccusiformis* Gayet & Meunier, 1996, *Inbecetemia torta* (Gayet & Meunier, 1996), *I. tortissima* (Gayet & Meunier, 1996), and *Nagaia extrema* nov. gen., nov. sp., occur in the Cenomanian of Sudan and in the Coniacian-Santonian of Niger (Table I). Therefore, these taxa show a long range. The living genus *Polypterus* can be traced back by two species, e.g., *P. dageti* and *P. sudanensis* nov. sp. to the earliest Late Cretaceous. Nevertheless, a more detailed study, compiling results of growth, histology, diversification and evolution of either fossil and recent polypterid pinnulae, scales, vertebrae and cranial fragments is in preparation (Gayet *et al.*).

Another occurrence of fossil polypterids represented by isolated scales and a cranial element was reported from the Cenomanian and the Eocene of Egypt (Stromer, 1936; Schaal, 1984). Moreover, there are records of polypterid fin spines from the Maastrichtian of Pajcha Pata and Vila Vila, and Early Late Paleocene of Tiupampa in Bolivia (Gayet and Meunier, 1991; Meunier and Gayet, 1996). All these records and mainly the high diversity of the family Polypteridae in the Cenomanian (Sudan and Egypt) emphasise that the evolutionary history of these fishes started at least in the Early Cretaceous period before separation of South America from Africa.

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